Decapod crustacean larval communities in the Balearic Sea (western Mediterranean): seasonal composition, horizontal and vertical distribution patterns

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Abstract

Decapod crustaceans are the main target species of deep water bottom trawl fisheries in the Balearic Sea but little is known about their larval stages. This work focuses on the species composition of the decapod larval community, describing the main spatio-temporal assemblages and assessing their vertical distribution. Mesozooplankton sampling was carried out using depth-stratified sampling devices at two stations located over the shelf break and the mid slope, in the north-western and southern of Mallorca in late autumn 2009 and summer 2010. Differences among decapod larvae communities, in terms of composition, adult's habitat such as pelagic or benthic, and distribution patterns were observed between seasons, areas and station. Results showed that for both seasons most species and developmental stages aggregated within the upper water column (above 75 m depth) and showed higher biodiversity in summer compared to late autumn. Most abundant species were pelagic prawns (e.g., Sergestidae) occurring in both seasons and areas. The larval assemblages' distributions were different between seasonal hydrographic scenarios and during situations of stratified and no-stratified water column. The vertical distributions patterns of different larval developmental stages in respect to the adult's habitat were analyzed in relation to environmental variables. Fluorescence had the highest explanatory power. Four clearly different vertical patterns were identified: two corresponding to late autumn, which were common for all the main larval groups and other two in summer, one corresponding to larvae of coastal benthic and the second to pelagic species larvae.

Key words: larval assemblages, Decapoda, adult habitats, developmental stage, vertical distribution patterns, western Mediterranean.

1. Introduction

Most species of decapod crustaceans produce planktotrophic pelagic larvae that in some areas and seasons can constitute a dominant group of the meroplankton (Beaugrand, 2005; Highfield et al., 2010). During their planktonic life they pass through many larval stages whose complexity varies among species, spending from hours to months in the pelagic environment before joining the parental population. Descriptions of decapod larvae communities are still rare for most places around the world (e.g., Brandão et al., 2012; Landeira et al., 2013). When available, they usually describe the nearshore communities (e.g., Fusté, 1982, 1987; Paula, 1987) because studies focusing on the spatial and temporal distribution of decapod larvae on estuarine or coastal waters are more accessible and hence monitoring less costly. Besides, there has been a worldwide interest to explain variations in larval supply rates in productive shelf areas, where physical processes such as seasonal upwelling can drive large larval mass to settle (e.g., Queiroga et al., 2007).

Decapod species associated with the continental shelf and slope tend to have a wide spatial offshore distribution, while those of coastal and nearshore species are usually found much closer to the coast (e.g., Dos Santos et al., 2008; Miller and Morgan, 2013). The temporal spawning patterns tend to vary among species with some species reproducing in cold, some in warm months and others all year around (e.g., González-Gordillo and Rodríguez, 2003; Pessani, 1993).

Decapod larvae feed on phytoplankton, detritus and other zooplankton (Anger, 2001). Therefore, we may expect rich communities of decapod larvae associated to areas of high primary productivity e.g. in coastal upwelling (Fusté and Gili, 1991) or in eddies around oceanic islands (Landeira et al., 2009, 2010). Surface fronts and mesoscale eddies may act as spatial hotspots of larval densities since these structures may increase the availability of trophic resources to biological organisms (Bakun and Weeks, 2006). Furthermore, protozoeal stages of the Dendrobranchiata are capable of retaining particles such as microorganisms, which can be crucial in oligotrophic waters where bacteria biomass is dominant over phytoplankton biomass and most carbon and nitrogen occur sequestered in bacteria (Cho and Azam, 1990).

Within the general oligotrophic environment of the western Mediterranean, the waters around the Balearic Islands show an even more pronounced oligotrophy (Bosc et al., 2004; Fernández de Puelles et al., 2007). However, the biological production around the Balearic Sea during summer is partly associated to mesoscale oceanographic features, fronts and eddies which may result in punctual productive zones (Alcaraz et al., 2007; Estrada et al., 1993; Jansà et al., 1998). This could explain the relatively high abundances of other meroplanktonic groups, as fish larvae, aggregating in the area, especially during summer (Alemany et al., 2006; Torres et al., 2011). Therefore, we may expect the presence of high abundances of decapod crustacean larvae as well. In the western Mediterranean, most surveys targeting meroplankton have been conducted during summer, when the water column is stratified with a well defined thermocline. Below the thermocline a deep chlorophyll maximum (DCM) is temporally found (Estrada et al., 1993; Jansà et al., 1998), coinciding with the maximum concentration of zooplankton (Alcaraz et al., 2007; Saiz et al., 2007). In Mediterranean waters few studies address together all groups that constitute the meroplankton concluding that their abundance in general decreases in autumn (e.g., Vives, 1966; Olivar et al., 2010).

In the Balearic Islands, the mesozooplankton community shows a clear seasonal pattern with highest abundances during summer and lowest numbers during winter. However, significant peaks can be recorded in autumn, mainly due to an increase in copepod abundances (Fernández de Puelles et al., 2003).

Some macro-zooplankton crustacean species are believed to be capable of utilizing dominant currents and maintain their vertical position in the water column to avoid food limitation in the general oligotrophic environment (Andersen et al., 2004). Vertical ontogenetic migration has been shown to play an important role in larvae of benthic species since they are hatched from eggs carried by bottom-dwelling females, after release into the water column they tend to feed in the upper layers and return to the adult habitat to settle. In the case of benthic species, an ontogenetic final migration from upper layers of the water column to settle in the bottom near adults' habitats is also well established (see review Queiroga and Blanton, 2004). Vertical migration behavior has been described for larvae that develop in estuarine, shelf, and oceanic waters (Queiroga and Blanton, 2004) and is considered to be mainly performed by the need to feed and, at the same time, avoid predation (Pearre, 2003).

In the western Mediterranean Sea some studies have considered the annual distribution of decapod larvae (e.g., Fusté, 1982, 1987; Pessani, 1993). Other studies have focused primarily on the summer season (Olivar et al., 1998). In an important area for crustacean fisheries, such as Balearic Islands, studies thus far have only focused on individual single species (Carbonell et al., 2010; Marco-Herrero et al., 2013; Torres et al., 2012; Torres et al., 2013).

The southern part of Balearic Islands, that forms part of the Algerian sub-basin, during summer, receives new lower salinity surface water from the Atlantic (AW) and the hydrodynamics of this area are thus strongly influenced by this density gradient. To the northern, the Balearic sub-basin consists of colder and more saline Atlantic surface waters that has remained longer in the Mediterranean (resident AW), and its dynamics is affected by notable atmospheric forcing, mainly wind. The Western Intermediate Water (WIW) is a modification of the Atlantic waters, formed only during winter in the Gulf of Lion and the northern continental shelves of the north-western Mediterranean (from the Ligurian Sea to the Catalan coast), and is not a consistent feature found every year around at the Balearic channels (Monserrat et al., 2008; Vargas-Yáñez et al., 2012). As a consequence, there are significant differences between the general hydrodynamic conditions that affect the north and the south of the islands.

The present study is the first specific research on the decapod larval community off the Balearic archipelago. Our aim is to describe seasonal patterns in the composition of the decapod larvae community and assess differences between the shelf break and the slope regions and between Balearic and Argelian sub-basins. We characterize these communities according to their adult habitats i.e. if the adult stages have a pelagic or benthic life mode, their taxonomic group and their larval development stage. Our hypothesis is that decapod larvae communities will be different for the two seasons and that both will be characterized mainly by larvae of pelagic species. In addition, the northern study area where the shelf is narrower and the slope is quite pronounced, the currents over the shelf created mixed conditions. In this case we expect to have an important component of larvae from coastal species in the northern stations, at least during warm season. Taking into account the resources availability for the oligotrophic

Mediterranean Sea we analyze and discuss environmental variables vertical distribution and their effect on the larval vertical distribution from pelagic or benthic adult's habitat in relation with the main oceanographic features of the area.

2. Material and methods

2.1. Sampling methodology

Two multidisciplinary research surveys were conducted off the Balearic archipelago (western Mediterranean; Fig. 1) during late autumn (29th November to 18th December 2009) and summer (11 to 30th July 2010) on board the R/V *Sarmiento de Gamboa*. We sampled a total of 4 stations during each cruise. One station was located over the shelf break (250 m depth) and the other over the mid slope (900 m depth) off the north-western (N), in Balearic sub-basin. The other two stations were also located in the shelf break and the mid slope but in the southern (S) of the Mallorca Island, in Algerian sub-basin. In each station we conducted repeated stratified hauls continuously during 36 hours. A total of 34 hauls resulting in 218 depth-stratified samples were sampled for decapod larvae. The hauls were distributed as: 5 hauls in the northern during late autumn, 13 hauls in the southern during late autumn, 8 hauls in the northern during summer and 8 hauls in the southern during summer (Fig. 1).

The samples were collected in late autumn using an HYDRO-BIOS MultiNet sampling five depth strata and in summer with a Multiple Opening-Closing Net and Environmental Sensing System (MOCNESS) sampling seven depth strata (Olivar et al., 2012). The net mouth openings were 0.25 and 1 m^2, respectively, and the mesh size was 333 μm for both nets. Both devices were towed at ~2 knots. The volume of water filtered in each layer varied from 44 to 2414 m^3, depending on the depth range of the layer sampled. The whole water column from a given depth relatively close to the bottom was sampled and the thickness of each layer varied depending on the bathymetry and the season (Table 1). Immediately after collection all samples were preserved in ~5 % borax-buffered formaldehyde, prepared using seawater. Once in the laboratory, samples were subsequently sorted for crustacean decapod larvae, which were identified to species level and developmental stage, whenever possible, using available descriptions (Dos Santos and Lindley, 2001; Dos Santos and González-Gordillo, 2004).

Geostrophic velocities at surface were obtained for both seasons from satellite altimetry data (Fig. 2a and 2b), which were downloaded from MyOcean (Bahurel et al., 2009). Delay Time data gridded into a Map of Absolute Dynamic Topography (DT-MADT) was used (Aviso, 2012). Hydrographic measurements were recorded using a CTD (SBE911) at the four plankton stations (Fig. 3a-3h). A salinity value of < 37.0 is the criterion used to identify the fresher Atlantic water (AW), and that of > 37.5 was used to identify resident AW. We refer to water with intermediate salinity values between 37.0 – 37.5 as mixed AW.

Vertical profiles of potential temperature, salinity and fluorescence were averaged at 1 m intervals to depict the vertical structure of the 200 first meters of water column and also $\theta - S$ diagrams were performed, based on potential temperature and salinity, to describe the water masses. The fluorescence concentration at the different depths was used as a proxy for food availability. Temperature values were used to describe the position of the thermocline and the thermal characteristics of the water column. Salinity was used to identify different water masses.

2.2. Spatial and seasonal larval distribution analysis

The species richness has been analyzed by means of dominance plots usually used to evaluate ecosystem status. Cumulative dominance percentage of species were calculated as the proportion of total hauls, by season, areas and sampling stations, where a species was present.

Density estimates of the organisms at each depth stratified sample were standardized to number of individuals per 100 m^3 at lowest taxonomic level identified, for each area and season. The frequency of occurrence of each taxonomic level was calculated. The species were grouped by their taxa group and their adult habitat to analyze their contributions to the larval community. Regarding their corresponding taxa group the decapod larval species were grouped in 7 categories as presented in Table 2 under the taxa column. According to their adult's habitat the larvae were assigned to 11 groups as presented in the column Adults Habitat in Table 2. To assess the vertical distribution of the larvae, besides the adult habitat classification we separated the larvae by ontogenetic developmental stage.

Differences in the composition of the assemblages of the larval community in the first 200 m, during late autumn and summer and at the four stations per season, were analyzed using nonparametric multivariate analysis applied to densities of the larvae (Clarke, 1993). Prior to the analysis, data were squared root transformed in order to prevent the dominant larval species from masking the responses of those with low densities (Clarke and Warwick, 2001). The Bray–Curtis similarity index was chosen as the similarity coefficient and the group average was used as the clustering algorithm (Clarke and Warwick, 2001). Cluster analysis and their corresponding two-dimensional representations by Multidimensional scaling ordination (MDS) were used to identify larval assemblages during both seasons. Stress coefficients with values <0.15 indicate that the data are portrayed well (Clarke and Gorley, 2006). We calculated the percentage contribution of average densities of the dominants groups by adult's habitat for main larval assemblage described by Cluster (SIMPER analysis).

Decapod larvae pass through several developmental stages that were merged in 2 groups to analyze their vertical distribution. A first group named *stage 1* included the first zoeal stages (Z) and a second group named *stage 2* included the advanced zoeal stages. The second developmental group (stage 2) never included megalopal or decapodite stages.

2.3. Vertical larval distribution analysis

The seasonal vertical distribution patterns for the main larval taxa belonging to the more representative adults' origin (coastal epibenthic, coastal nektobenthic, epipelagic and mesopelagic) were analyzed within the first 200 meters of the water column, where most decapod larvae were found (up to 90.7 % and 93.7 % of the total density in autumn and summer, respectively). General Linear Models (GLMs) were used to analyze the environmental variables that could drive the larval vertical distributions. Temperature, salinity and fluorescence were used as continuous co-variables and larval density as the independent variable. Area (northern and southern) and station (shelf break and mid slope) were included in the model as factors.

3. **Results**

3.1. Hydrographic conditions

In the upper layers, during late autumn, a well defined anticyclonic gyre at the north of Ibiza deflected Northern Current waters (Fig 2a). The southern area was mainly under the influence of a cyclonic gyre formed by resident Atlantic waters (AW) re-circulated from the Balearic sub-basin and flowing from coastal areas at the east of Mallorca (Fig. 2a). During summer, we observed an anticyclonic gyre in the northern area, but situated slightly northwards and affecting mostly the slope and a cyclonic meander to the south-western. In contrast, the southern area was mostly occupied by an anticyclonic gyre of recent Atlantic Waters, detached from the main current of recent Atlantic Waters flowing in SW-NE direction at the south of the archipelago, trapped at the east of Ibiza Island (Fig. 2b). The geostrophic currents during late autumn reached higher values than during summer (Fig. 2a and 2b).

Therefore, there were contrasting hydrographic conditions between the late autumn and summer seasons (Fig. 2 and 3) due to (a) the income of new AW in the upper layers in summer, (b) the seasonal differences in the presence / absence of Western Intermediate Waters (WIW) and (c) the stratification of the water column (Fig. 3). The water masses found at the surface during both surveys were different. Thus, during late autumn we could find only resident surface Atlantic Waters in both areas (Fig. 3a) whereas in summer we also observed mixed Atlantic waters in the southern (Fig. 3b).The seasonal differences in WIW are clearly observed in the $\theta - S$ diagrams, indicating absence of WIW (Fig. 3a) during autumn, whereas during summer three of the stations showed the presence of WIW (Fig. 3b).

The water column was stratified in summer whereas in late autumn conditions were of mixed layer without clear clines. More specifically, the temperature in the upper layers was colder in late autumn, around 17ºC, whereas in summer temperatures up to 26ºC and 27ºC were recorded (Fig. 3c and 3d). In late autumn the surface waters were saltier (~38) than during summer, when the income of recent AW resulted in the presence of less saline waters (37.5 – 37.9) (Fig. 3e and 3f). Regarding surface fluorescence values, in autumn (range between 0.1 – 0.3; Fig. 3g) were higher than in summer (~0.05; Fig. 3h). The vertical profiles of the environmental variables during the late autumn survey were homogeneously distributed down to the mixing layer depth (MLD), located at 60 and 80 m depth in the southern and the northern, respectively (Fig. 3c, 3e and 3g).

In summer, environmental variables showed strong gradients in the upper 100 meters. A shallow MLD of around 10-13 m and a thermocline located between 10 to 50 m depth was observed in the summer, in both areas (Fig. 3d). During late autumn no halocline was detected and in summer halocline was located between 5 to 25 m depth, when surface waters were influence by wind (Fig. 3e and 3f). Deep fluorescence maximums with values between 0.4 and 1 were found below the MLD between 50 and 80 m depth in summer (Fig. 3h). The maximum fluorescence peak was located over slope in the southern study area, at 80 m depth, and the minimum in northern area also over the slope, at 55 m depth, which in addition represented the shallowest registered depth of such fluorescence peak.

3.2. Assemblage composition, seasonal and horizontal larval distribution

The list of all taxa identified in the samples with total individuals identified for each season and the mean densities for same season and in the same area are given in Table 2. From the total of 121 taxa found, 19 were identified at family level (or higher), 27 at genus level and 75 at species level. Most of them appeared only in summer (63), whereas only 7 were exclusively present in late autumn. In terms of the main decapod taxa groups, the most abundant in the samples were shrimps (Dendrobranchiata) larvae that accounted for 63 % of the total decapod larvae sampled during late autumn and 52 % in summer, followed by crabs species (Brachyura) for late autumn, with 18 %, and in summer by caridean shrimps, with 32 %. The minor groups during both seasons were, in order of abundance, hermit crabs, squat lobsters, slipper lobster and ghost shrimps. Regarding the origin of the larvae, they were mainly constituted by species from mesopelagic and epipelagic habitats, comprising around 57 % of the total captures.

Shrimps larvae during autumn were mainly *Gennadas elegans*, whereas in summer *Parasergestes vigilax* and *Eusergestes arcticus* were the most abundant ones. Mean densities of *G. elegans* during late autumn were about 14.5 ind. per 100 m^3 (±8.7) in northern stations to 6.1 ind. per 100 m^3 (±3.8) in southern stations (Table 2). The crab species *Goneplax rhomboides*, second in order of abundance during the fall season, appeared only in the southern, with mean abundances of 2.9 ind. per 100 m^3 (±4.3). *E. arcticus* and *Plesionika* spp. registered important abundances as well in this season. The summer most abundant species was *Parasergestes vigilax,* showing densities from 1.8 ind. per 100 m^3 (±2.6) in the northern area to 2.2 ind. per 100 m^3 (±3.4) in the southern. Three crab taxa exclusively found in summer and relatively abundant were *Parthenope* spp., *Ebalia* spp. and *Xantho* spp., followed by hermit crabs such as *Calcinus tubularis*.

The species rank plots showed that the decapods larval community was most diverse during summer, especially in the northern area, and higher species dominance were registered in late autumn (Fig. 4). In late autumn, the southern area showed the highest diversity, having the "southern shelf break" station similar species richness, as the ones found at summer stations.

The analysis of the horizontal distribution of larvae grouped considering the adult's habitats showed no clear pattern between areas. During late autumn the larvae were mainly from mesopelagic species, which dominated in the northern area, whereas in the southern a mixed assemblage was observed, with high percentage of larvae from coastal epibentic species (Table 3). In summer, at the northern area the assemblage was mixed, with larvae from all types of species, whereas in the southern area the community was mainly constituted by larvae belonging to pelagic, coastal necktobenthic and oceanic epibenthic species (Table 3). Moreover, significant differences between seasons, areas and station for the second group of development stage were detected for larvae from coastal epibenthic and nektobenthic adult's, which are summarized in Table 4. Furthermore, for the first group of development stage differences between area and station were significant for late autumn for pelagic and for pelagic and coastal species at summer (Table 5).

The inter-relationships by season, determined by means of the cluster analysis considering the available data from the hauls carried out at different depth ranges between 0 and 200 m, are presented in Fig. 5a and 5c. The SIMPER analysis was used to identify those adults habitats, used as a proxy for the origin of the larvae, primarily responsible for the differences among larval assemblages. The adult habitats explained

more than 50 % of the analyzed cluster variability. In both seasons, larvae from mesopelagic species were the dominant group, despite the larvae of epipelagic species were also important in summer (Table 3). The "late Autumn Southern shelf break" cluster group (ASshelf; Fig. 5a, b) was the most diverse, with a predominance of coastal benthic species (epibenthic plus necktobenthic) and with an important contribution of mesopelagic species. Nevertheless, the rest of the hauls in "late Autumn" (A; Fig. 5a, 5b) were clearly dominated by larvae of mesopelagic species. At "Summer the Southern slope" Cluster assemblage (SSslope; Fig. 5c, d) grouped hauls from southern slope, whereas the rest of summery hauls were grouped in the "Summer" cluster assemblage (S; Fig. 5c, d). The similarity analysis for summer season revealed that about 50 % of the variability was explained by larvae from coastal benthic species (coastal epibenthic and necktobenthic), grouped in summer cluster assemblage "S", except in the "Summer Southern slope" cluster assemblage "SSslope", which was exclusively formed by larvae of mesopelagic and epipelagic species.

3.3. Vertical larval distribution

A general vertical distribution pattern, characterized by the aggregation of individuals within the upper 75 m of water column, was followed by all taxa and larval stages. However, two different vertical distribution patterns were identified in each season for the main larval groups according to the adult's habitat and the larval developmental stage.

For late autumn, the non-stratified season, the general pattern (pattern 1) shows that the larvae were mainly concentrated at depths between the 25 and 75 m. It happened in both zoeal groups (pattern 1a, see Fig. 6a, 6c and pattern 1b, see Fig. 7c), being fluorescence the variable that explained most of the vertical distribution variability (Fig. 6b, 6d, 7d). However, during late autumn this pattern differed for stage 1 (early protozoeae) by larvae belonging to pelagic species, which were mainly found between 60 and 200 m depth (pattern 2 see Fig. 7a) and showed a strong relation to temperature and salinity (Fig. 7b).

In addition, during fall season in southern area the highest densities of early zoeae of coastal benthic species were situated over shelf break (Fig. 7c). At this station (southern shelf break) the temperature and fluorescence presented the highest values during the season (Fig. 3d, 3f) coinciding with the depth of densities' peak of larvae (around 25-75m). At this point we found the highest abundances of developmental larval group 1 from coastal epibenthic and nektobenthic taxa, composed mainly by *Goneplax rhomboides* and *Plesionika* spp*.,* respectively.

During summer, when the water column was stratified, showing a marked thermocline, halocline and fluorescence peak, two different patterns were identified also. All larval stages of coastal epibenthic and nektobenthic species presented a decreasing density from surface down to 75 m (pattern 3, see Fig. 6f, 7g). Temperature, salinity and fluorescence explained the stage 2 (late zoeae) distribution pattern (Fig. 6g). For the stage 1 group, fluorescence and salinity were the main variables explaining the vertical distribution of the larvae (Fig.7h), corresponding to the minimum observed values, recorded at surface, to the maximum larval abundance.

The larvae of the mesopelagic and epipelagic species showed two clear peaks in summer (pattern 4), one at the surface layers, from 0 m to 25 m depth, and the other from 50 m to 75 m depth (Fig. 6e, 7e). The surface peak was mainly attributable to *Parasergestes vigilax*, and was best explained by temperature, suggesting that these larvae preferred warm waters above the thermocline. On the other hand, fluorescence was the environmental variable that best explained the deep peak, where the main abundances were of *Eusergestes arcticus*, suggesting that these larvae concentrate at the maximum fluorescence peak (Fig. 7f).

The highest larval abundances in late autumn were registered at the southern shelf break station. The highest values of temperature and fluorescence during late autumn at this station (17.6 ºC and 0.43, Fig. 3c, 3g) agree well with the depth in which the highest densities of larvae were found (around 25-75 m, Fig. 6 and 7). The highest abundances in summer were found at the surface layers of the northern mid slope station (Fig. 6 and 7). The highest values of temperature during warm season (27 ºC; Fig. 3d) at this station agree with the depth in which the highest densities of larvae were registered.

4. **Discussion**

4.1. *Seasonal and horizontal larval distribution*

We found decapod larval densities around 100 times lower than those reported for productive upwelling nearby coastal Atlantic areas (e.g., Dos Santos et al., 2008; Fusté and Gili, 1991). This agrees well with the oligothrophic characteristics of the Mediterranean Sea nevertheless the sampled area of the present study is located on the shelf break where recurrent mesoscale eddy activity is observed. However, late autumn larval densities were similar to those found off Canary Islands (23.7 ind. per 100 m^3 ± 22.9; Landeira et al., 2010). This could be related to the 'island mass effect' (Doty and Oguri, 1956), which cause and enhancement of primary productivity around islands in relation to open ocean waters (Gilmartin and Revelante, 1974; Hernández-León, 1991), increasing preys availability and, in consequence, we could expect higher abundances of decapod larvae. Mesoscale oceanographic features such as fronts and eddies are key mechanisms to enhance the biological productivity in specific areas (Alcaraz et al., 2007; Estrada, 1996). The Balearic Sea, due to the interaction among different water masses and of those with the island's topography, is a hydrodinamically complex area (López-Jurado et al., 1995, 1996; Pinot et al., 2002). Moreover, we found the maximum peak of larval density during summer in the northern area, associated to strong geostrophic currents and an anticyclonic eddy. The continuous current system that runs from the mainland to the Balearic archipelago in some years could result, in local enrichment processes derived from the more productive area linked to the Spanish mainland rivers (López-Jurado et al., 2008; Pinot et al., 2002).

The dominance of shrimps (Dendrobranchiata species) in our assemblages is in agreement with those observed for offshore waters around oceanic islands (e.g.,Brandão et al., 2012 off Saint Paul's Rocks, Southwest Atlantic Ocean; Landeira et al., 2009 off Canary Islands). On the contrary, crab larvae usually dominate decapod larvae assemblages from continental shelf areas (e.g., Dos Santos et al., 2008) or neritic areas around Atlantic islands (Koettker and Freire, 2006). In our study, crabs were the second most abundant group during late autumn and the third in summer, suggesting some degree of mixing between typical offshore, such as mesopelagics, and nearshore, such

as coastal-benthic species. Specifically, information on the casual occurrence and morphology of larval stages of the red shrimp *Aristeus antennatus*, the rose shrimp *Parapenaeus longirostris*, the slipper lobster *Scyllarides latus* and the Mediterranean spider crab *Maja squinado*, species that are important for fisheries management and conservation purposes have been published recently (Torres et al., 2013).

The most abundant taxon in our samples at late autumn, *Gennadas elegans* (Dendrobranchiata), presented its highest densities at the northern of the Balearic Islands (14.5 ind. per 100 $m^3 \pm 8.7$) coinciding with the highest velocity currents. This high density in Balearic oligotrophic waters could be explained by the capacity of Dendrobranchiata early life stages to retain picoplankton which tend to dominant over phytoplankton biomass. Thus picoplankton could act as source for carbon and nitrogen (Cho and Azam, 1990). It must be pointed out that in autumn the maxima of dissolved organic carbon are found in surface waters, where it is continuously removed from surface waters by diffusive processes during the stratified period in north-western Mediterranean (Copin-Montégut and Avril, 1993).

A review of the relevant literature shows that Mediterranean pelagic shrimps have not been thoroughly studied and information on their adult distribution is poor (e.g., Casanova, 1977; Koukouras, 2000; Koukouras et al., 2000). Within this context, the present study allows us to reveal some ecological traits for these pelagic species that currently are of no commercial interest to the fishing industry and for which no previous information of this type exists for the western Mediterranean (Simão et al., 2013-this issue).

According to Champalbert (1996) zooplankton communities in the western Mediterranean present low diversity at inshore waters, especially when the continental shelf is narrow. Contrastingly, in our case decapod larval k-dominance curves showed different behavior, in the northern shelf in summer, since our highest diversity and density values were registered there, despite the shelf is narrower than in the southern area. The larvae of coastal nektobenthic and epibenthic species dominated the decapod larvae community in this area and season, showing the maximum values of biodiversity registered for Mediterranean Sea (Fusté, 1987; García-Comas et al., 2011; Pessani, 1975). In late autumn larvae of these groups dominated also the communities over the shelf break in the southern part of the Balearic Islands. However, overall the larvae of pelagic species dominated in the majority of our samples, comprising 57 % of total decapod larvae.

Our data revealed the highest densities and biodiversity of decapod larvae in summer, coinciding with the major reproductive season for most decapods species in the western Mediterranean (García Raso, 1982; Zariquiey, 1968). The seasonal pattern described for pelagic shrimps (Dendrobranchiata and Caridea) larvae agrees with the seasonality in species composition of the neighboring Ligurian Sea, where the species maximums were registered in June and the minimum in autumn-winter (Pessani, 1993). As mentioned above, in our samples taken off the Balearic Islands, the most abundant species were the mesopelagic shrimp *Gennadas elegans*. In a study carried out on the shelf of Catalonian coast all the year round, *G. elegans* larvae showed their maximum abundance during February, and the minimum in October, but no larvae were found in December and July (Fusté, 1987). On the contrary, we registered the presence of *G. elegans* larvae in both months, being present in abundance in December. Therefore we

441 can conclude that this species reproduces during all year in the western Mediterranean,
442 and that late autumn – winter potentially being their most important reproductive
443 season.

444 4.2. *Hydrographic effect on larval assemblages*

445 Larval densities during the autumn season differed between the two study zones
446 (northern and southern). The highest densities were observed in the southern shelf break
447 and the lowest at the northern slope stations. The larval assemblages were mainly
448 constituted by larvae of mesopelagic species, except for the southern shelf break station,
449 where coastal benthic species larvae dominated. The observed differences were
450 probably related with the currents registered in the area.

451 There was a strong north-south flowing current during late autumn, originated in
452 offshore areas of Balearic sub-basin and associated to a front perpendicular to the shelf
453 located in the northern sampling area, which swept both northern area and southern
454 slope stations (Balbín et al., 2012). This current could explain why the majority of
455 decapod larvae at the northern and in the outer southern stations (autumn cluster group)
456 belonged to mesopelagic species. The larvae of coastal benthic species were
457 concentrated over the southern shelf break station (Autumn Southern shelf cluster
458 group) where a cyclonic gyre could promote its retention. Species richness and also
459 larval densities were highest at this southern shelf break station. This fact could also be
460 a consequence of the aforementioned gyre; it not only would retain larvae, but would
461 produce the mixing of larvae of more coastal and deeper upper slope species, increasing
462 the diversity of such mixed larval assemblage.

463 In summer, both the northern stations and the southern shelf break station with a high
464 similarity, showed a mixed larval assemblage, and composed by mesopelagic,
465 epipelagic and coastal necktobenthic species, without any clear dominance of one group
466 over the others. On the contrary, almost only larvae from pelagic species were found at
467 the southern slope station coinciding with an anticyclonic input of lower salinity
468 Atlantic, since up to 80 % of specimens were *Parasergestes vigilax* early protozoeae
469 (stage 1). Most of the late protozoeae of this species were caught over the northern
470 slope, in the front side of an anticyclonic eddy.

471 Currents in summer were in general less intense than in late autumn, which could allow
472 spatial retention of larvae close to the area of their release. However, in the northern
473 area, the cyclonic gyre located over the shelf break sampling station should promote the
474 advection of coastal larvae to the nearby offshore stations, favoring the existence of the
475 mixed assemblage with the highest biodiversity. In fact, in the north of Mallorca where
476 the shelf is narrower and the slope is quite pronounced, the currents over the shelf
477 created mixed conditions, that could explain the important component of larvae from
478 coastal species. Specifically, over the northern shelf break the highest larval densities of
479 *Plesionika* spp. and *Xantho* spp. swept from coastal benthic zones were caught. In the
480 northern slope station, the only with surface resident AW, had been influenced by a
481 heavy anticyclonic feature which would also favour the mixing of larvae. The highest
482 larval density value was registered, corresponding mainly to larvae of epipelagic adults
483 (e.g., Sergestidae), as those of *P. vigilax* mentioned above.

Mesoscale advective processes (surface fronts and eddies) affect planktonic communities and may offer opportunities for exceptional local productivity and growth of species. Owing to the complex hydrodynamic situation and topographic features in the study area, mesopelagic species were also relatively abundant in stations located over the shelf break, being found together with larvae of neritic species.

The general structure of decapod larvae community found off the Balearic Islands is similar to that reported in nearby Spanish continental coast by Fusté (1987), with pelagic taxa being more dominant. The mesopelagic species dominance during both seasons in our study area was expected as all sampling stations were not located close to the shore, the shelf in this area is relatively narrow and hence the distance between shelf break and slope stations is short, and also because the existence of mesoscale features as eddies favor the advection of offshore species larvae to shelf.

4.3. Environmental effect on vertical larval distribution

Most decapod larvae were distributed between the 0-75mand followed well the vertical pattern in fluorescence during both seasons. The early and late protozoeae are mostly phytotrophic and they can adapt their movements in the water column to stay by the fluorescence peak and optimize their feeding. Increasing food abundance enhances feeding rates and resulting developmental rates in decapod larvae (Dawirs, 1985). Therefore, observed larval distribution may reflect an optimization of their behavior in the water column to favor the encounter of food. Decapod larvae show positive phototaxis in the laboratory (e.g., Sulkin, 1975), which is supported by the finding of the current study that found mainly larvae within the euphotic layer (0 – 200 m).

The earliest stages of the pelagic species (mesopelagic and epipelagic) in late autumn were distributed between the 60-200 meters. These developmental stages could have been caught during their first ontogenetic migration upwards from the deepest layers were they were probably born since the adults of these species, e.g., *Gennadas elegans,* are mostly located in the mid slope within the Deep Scattering and the Benthic Boundary Layers around 400 m depth close to the bottom (Ramón et al., 2013-this issue; Simão et al., 2013-this issue). Another example is the case of *Eusergestes arcticus*. The adults inhabit the mesopelagic waters whereas the larvae were located mostly between 50-75 m depth. For the epipelagic shrimp *Parasergestes vigilax* most larvae were located in the first 25 m of the water column.

Crustacean larvae are able to swim across environmental gradients in the water column such as the thermocline (Dos Santos et al., 2008; Lindley et al., 1994). They can perform diel vertical migrations though patterns can vary among the successive developmental stages and species (e.g., Andersen et al., 2004; Dos Santos et al., 2008; Lindley et al., 1994). We have observed larvae above the thermocline during the summer supporting these previous findings. Though some of the larvae were found at the highest temperatures, most larvae were not located in the warmest layers. The occurrence of the larvae of the same species across temperatures ranges of 13-27 ºC reinforces the conclusion that temperature is not a main variable defining the vertical distribution of the early life stages of decapod crustaceans.

Migratory behavior in crustacean larvae has been related to predator-avoidance, hunger and adaptations to optimize dispersal by currents (Queiroga and Blanton, 2004;

Landeira, 2009; Pearre, 2003). At surface, potential predators such as fish larvae (Olivar et al., 2013-this issue) coexist with crustacean larvae. On the other hand, late stages can predate on zooplankton while earlier stages prey mostly on phytoplankton. The vertical position of the crustacean larvae may reflect strategies considering a trade-off between the optimization of food availability and survival. Further research on the overlap in the water column of crustacean and fish larvae can help to describe such trade-offs.

5. Conclusions and perspectives

Our study provides for the first time an accurate analysis of the decapod larvae structure and vertical distribution over shelf break and mid slope in two seasons at two areas off the Balearic Islands. The community of decapod larvae in the study area is composed mainly of larvae of mesopelagic shrimp species (Dendrobranchiata). Our results show also that the complex surface water circulation patterns around the Balearic Archipelago, characterized by the presence of mesoescale structures as fronts and eddies, can lead to local larval retention over the adult populations. The oceanography causes the mixing of coastal and mesopelagic species larvae in the area.

The analyses of the vertical distribution of larvae show most larvae concentrate in the first 75 m of the water column thought differences are observed among species mostly related to the vertical distribution of different ontogenetic developmental stages. The main factor explaining the observed vertical distributions is food availability. The larvae are concentrated in the depth ranges of the water column where the fluorescence values confirm higher concentration of potential preys, considering that decapod larvae feed on picoplankton and phytoplankton. Within this context, the vertical position of the crustacean larvae may reflect strategies considering a trade-off between the optimization of food availability and survival. However, further improvements on the knowledge of ecology and vertical distribution of autotrophic and heterotrophic plankton, communities are deemed necessary in the area to achieve a better understanding of the biological processes affecting decapod larvae survival.

The positioning of the larvae along the water column could be related to species specific strategies developed to optimize recruitment processes, since transport of decapod larvae throughout their pelagic larval stages is a key determinant of adult population dynamics. The larval vertical migration behaviors may couple with vertically stratified flows to retain larvae nearshore. Thus, by varying their vertical position in relation to mesoescale hydrological structures, they could control in a certain way their transport from spawning to nursery areas. In order to identify better their effect on life history traits our results underline the need for further detailed studies, with new data taken concurrently on both physical and biological parameters. These kinds of studies would allow developing biophysical models which require not only accurate 3D hydrodynamic models but reliable information on larval distribution, ecology and behavior. Thus, the knowledge on larval assemblage's structure, distribution and ecology will be essential in improving our understanding of population's dynamics and population connectivity aspects that will be important to inform management strategies.

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808

809 **Figure legends:**

810 Fig. 1. The study area and main hydrographic features. The Mallorca and Ibiza
811 channels, the Northern and Balearic Currents, and the Algerian Gyres are indicated.
812 Study area (framed and dotted) with haul's position during late autumn (A) 2009 (black)
813 and summer (S) 2010 (grey), at four plankton stations located over shelf break (250
814 isobath) and mid slope (900 isobath) off the northwest(N) (Balearic sub-basin) and
815 southern (S)(Algerian sub-basin) of Mallorca Island. Grey lines indicate isobaths (200,
816 400, 600, 800 and 1000 m).

817 Seasonal stations symbols: (Δ) Northern shelf break; (+) Northern mid slope; (♦) Southern shelf break; (□) Southern mid slope.

818

819 Fig. 2. Map of absolute dynamic topography and surface derived geostrophic currents at
820 study area during late autumn in 2009 (a) and summer in 2010 (b) with hydrographic
821 stations and structures (A: Anticyclonic eddie; C: Cyclonic eddie)

822 Stations symbols: (Δ) Northern shelf break; (+) Northern mid slope; (♦) Southern shelf break; (□) Southern mid slope

823 Fig 3. Seasonal θ – S diagram with gray boxes indicating the different water masses (a,
824 b), potential temperature (c, d), salinity (e, f) and fluorescence (g, h) vertical profiles at
825 four stations. For TS profiles below 50 m to bottom were plotted and the rest of
826 variables from surface down to 200 m.

827 Stations lines: black: Northern mid slope; black dotted: Northern shelf break; gray: Southern mid slope; gray dotted: Southern shelf
828 break

829 Water masses: Levantine Intermediate Water (LIW), Western Mediterranean Intermediate Water (WIW) and Western Mediterranean
830 Deep Water (WMDW)

831 Fig. 4. Multiple k-dominance curves with cumulative dominance percentage of species
832 described at four plankton stations during late autumn (black) and summer (grey).

833 Seasonal stations symbols: (Δ) Northern shelf break; (+) Northern mid slope; (♦) Southern shelf break; (□) Southern mid slope.

834 Fig. 5. Seasonal cluster analysis (on the left) and Multidimensional scaling (MDS) of
835 BrayCurtis similarities (on the right) of hauls based on adults habitat densities and their
836 assemblages at 50 % similarity during late autumn (a and b) and 65 % during summer (c
837 and d). Clusters groups in bubbles, two during late autumn (AS shelf: late Autumn
838 Southern over shelf break; A: Autumn rest of the samples) and other two during summer
839 (S: Summer rest of the samples; SS slope: Summer Southern over mid slope). Samples
840 legends N: Northern stations and S: Southern stations.

841 Seasonal stations symbols: (Δ) Northern shelf break; (+) Northern mid slope; (♦) Southern shelf break; (□) Southern mid slope.

842 Fig. 6. Scatterplots of observed (a, c, e, f) and predicted (b, d, g) larval densities (n/m^3)
843 with explanatory variables, of adult habitat epipelagic (Ah_7), mesopelagic (Ah_8),

coastal epibenthic (Ah_3) and coastal nektobenthic (Ah_4) of late development stage group (stage 2), at four plankton stations during autumn and summer. Environmental variables fluorescence (fluo), temperature (temp) and salinity (sal).

Stations symbols: (Δ) Northern shelf break; (+) Northern mid slope; (♦) Southern shelf break; (□) Southern mid slope. nd= not enough data

Fig. 7.Scatterplots of observed (a, c, e, g) and predicted (b, d, f, h) larval densities (n/m^3) with explanatory variables, of functional groups epipelagic (Ah_7), mesopelagic (Ah_8), coastal epibenthic (Ah_3) and coastal nektobenthic (Ah_4) of group 1 of early stages (stage 1), at four plankton stations during autumn and summer. Environmental variables fluorescence (fluo), temperature (temp) and salinity (sal).

Stations symbols: (Δ) Northern shelf break; (+) Northern mid slope; (♦) Southern shelf break; (□) Southern mid slope

TABLES

Late autumn (2009)		Summer (2010)	
Shelf break (m)	**Mid slope (m)**	**Shelf break (m)**	**Mid slope (m)**
0-30	0-60	0-25	0-25
30-60	60-200	25-50	25-50
60-90	200-350	50-75	50-75
90-120	350-600	75-100	75-125
120-200	600-850	100-125	125-200
		125-150	200-400
		150-200	400-500

Table 1. Depth strata level with the thickness of each layer in meters during the late autumn and summer surveys over the shelf break and the mid slope stations.

Taxa	Adults Habitat	Late autumn N	Late autumn Northern F (%)	Late autumn Northern ρ ± SD	Late autumn Southern F (%)	Late autumn Southern ρ ± SD	Summer N	Summer Northern F (%)	Summer Northern ρ ± SD	Summer Southern F (%)	Summer Southern ρ ± SD
SHRIMPS (Dendrobranchiata)											
**Allosergestes sargassi*	mesopelagic						7	50.00	0.02 ± 0.02	50.00	0.01 ± 0.02
**Aristeus antennatus*	oceanic epibenthic						3	25.00	0.01 ± 0.02	25.00	0.01 ± 0.01
^Dendrobranchiata n. id.	-	1	20.00	0.02 ± 0.05							
Deosergestes corniculum	epipelagic	2			15.38	0.02 ± 0.05	70	100.00	0.14 ± 0.11	75.00	0.12 ± 0.22
Deosergestes henseni	mesopelagic	2	20.00	0.02 ± 0.05	7.69	0.01 ± 0.05	162	87.50	0.26 ± 0.25	100.00	0.48 ± 0.55
Eusergestes arcticus	mesopelagic	256	100.00	3.92 ± 2.98	61.54	0.46 ± 0.51	616	100.00	1.94 ± 2.61	100.00	0.97 ± 0.87
Gennadas elegans	mesopelagic	1445	100.00	14.53 ± 8.73	100.00	6.05 ± 3.81	132	75.00	0.10 ± 0.11	100.00	0.57 ± 0.50
**Lucifer typus*	epipelagic						1	12.50	0.01 ± 0.01		
Parapenaeus longirostris	oceanic epibenthic	1	0.00		7.69	0.01 ± 0.05	1			12.50	0.01 ± 0.02
Parasergestes vigilax	epipelagic	4	20.00	0.04 ± 0.08	23.08	0.03 ± 0.06	887	100.00	1.77 ± 2.67	100.00	2.21 ± 3.43
Sergestes atlanticus	epipelagic	12	20.00	0.28 ± 0.64	23.08	0.04 ± 0.09	23	62.50	0.05 ± 0.06	62.50	0.04 ± 0.04
Sergestes spp.	epipelagic	12	40.00	0.05 ± 0.06	46.15	0.13 ± 0.18	277	100.00	0.72 ± 0.33	87.50	0.49 ± 0.48
Sergestidae n.id.	-	116	100.00	1.83 ± 0.68	53.85	0.29 ± 0.39	97	87.50	0.23 ± 0.37	100.00	0.26 ± 0.17
Sergia robusta	mesopelagic	140	80.00	2.35 ± 3.03	69.23	0.47 ± 0.47	160	87.50	0.49 ± 0.54	87.50	0.20 ± 0.20
**Sergia splendens*	mesopelagic						2	12.50	0.01 ± 0.03		
Sergia spp.	mesopelagic	22	80.00	0.44 ± 0.48	23.08	0.03 ± 0.06	1	12.50	0.01 ± 0.01		
Solenocera membranacea	coastal nektobenthic	28	20.00	0.05 ± 0.11	69.23	0.32 ± 0.37	126	100.00	0.52 ± 0.66	50.00	0.24 ± 0.28
CARIDEAN SHRIMPS (Caridea)											
Acanthephyra spp.	meso/bathypelagic	27	80.00	0.32 ± 0.36	76.92	0.17 ± 0.17	102	87.50	0.36 ± 0.22	75.00	0.05 ± 0.06
**Aegaeon spp.*	cosmopolite epibenthic						22	62.50	0.12 ± 0.15	25.00	0.02 ± 0.04
Alpheus glaber	cosmopolite nektobenthic	32	40.00	0.05 ± 0.08	53.85	0.44 ± 0.63	144	87.50	0.54 ± 0.46	75.00	0.22 ± 0.24
Alpheus spp.	cosmopolite nektobenthic	10			30.77	0.13 ± 0.35	185	100.00	0.61 ± 0.96	50.00	0.05 ± 0.11
Athanas nitescens	coastal epibenthic	7	20.00	0.01 ± 0.03	30.77	0.11 ± 0.17	24	75.00	0.09 ± 0.15	25.00	0.04 ± 0.07
^Brachycarpus biunguiculatus	coastal epibenthic	1			7.69	0.02 ± 0.07					
Caridea n. id.	-	12			23.08	0.08 ± 0.17	5	12.50	0.01 ± 0.02	37.50	0.02 ± 0.04
**Caridion steveni*	coastal epibenthic						1			12.50	0.01 ± 0.02
**Chlorotocus crassicornis*	oceanic epibenthic						1	12.50	0.01 ± 0.02		
Eualus cranchii	coastal epibenthic	3			23.08	0.05 ± 0.10	45	75.00	0.17 ± 0.32	37.50	0.11 ± 0.16
**Eualus occultus*	coastal epibenthic						7	25.00	0.04 ± 0.10	12.50	0.01 ± 0.02
Eualus spp.	coastal epibenthic	1			7.69	0.02 ± 0.08	28	75.00	0.05 ± 0.04	50.00	0.11 ± 0.18
Hippolytidae n.id.	coastal epibenthic	8	20.00	0.02 ± 0.05	46.15	0.08 ± 0.11	24	75.00	0.10 ± 0.13	62.50	0.05 ± 0.06
**Lysmata seticaudata*	intertidal nektobenthic						1	12.50	0.01 ± 0.01		
**Lysmata spp.*	intertidal nektobenthic						20	75.00	0.08 ± 0.07	12.50	0.01 ± 0.01
**Palaemon elegans*	intertidal nektobenthic						1	12.50	0.01 ± 0.02		
**Palaemon macrodactylus*	intertidal nektobenthic						7	12.50	0.02 ± 0.06		
**Palaemon spp.*	intertidal nektobenthic						1	12.50	0.01 ± 0.01		
*Palaemonidae n.id	intertidal nektobenthic						1	12.50	0.01 ± 0.02		
Pandalidae n.id.	-	9			38.46	0.09 ± 0.19	44	87.50	0.12 ± 0.12	75.00	0.14 ± 0.18
Pandalina brevirostris	coastal nektobenthic	8			46.15	0.09 ± 0.12	78	62.50	0.35 ± 0.47	87.50	0.15 ± 0.13
**Pasiphaea sivado*	cosmopolite epibenthic						3	25.00	0.01 ± 0.02	12.50	0.01 ± 0.02
^Philocheras echinulatus	oceanic epibenthic	6	20.00	0.04 ± 0.08	30.77	0.09 ± 0.17					
**Philocheras fasciatus*	intertidal epibenthic						2	25.00	0.01 ± 0.02		
Philocheras sculptus	coastal epibenthic	5			38.46	0.09 ± 0.12	3	12.50	0.01 ± 0.04	12.50	0.01 ± 0.02
^Philocheras spp.	oceanic epibenthic	2			7.69	0.04 ± 0.16					
Philocheras trispinosus	intertidal epibenthic	2			15.38	0.03 ± 0.08	1	12.50	0.01 ± 0.02		
*Pleocyemata n. id.	-						1			12.50	0.01 ± 0.02
Plesionika spp.	coastal nektobenthic	103	60.00	0.11 ± 0.12	100.00	1.54 ± 1.85	370	100.00	1.32 ± 1.33	100.00	0.85 ± 1.03
**Pontonia spp.*	coastal epibenthic						3	12.50	0.01 ± 0.01	12.50	0.01 ± 0.02
*Pontoniinae n.id.	coastal epibenthic						14	50.00	0.04 ± 0.06	50.00	0.02 ± 0.03
Processa canaliculata	oceanic epibenthic	6	40.00	0.04 ± 0.05	23.08	0.06 ± 0.13	42	62.50	0.29 ± 0.40	12.50	0.01 ± 0.02
Processa edulis edulis	intertidal epibenthic	13			53.85	0.20 ± 0.24	51	100.00	0.25 ± 0.23	50.00	0.03 ± 0.05
**Processa macrodactyla*	coastal epibenthic						5	25.00	0.04 ± 0.08		
**Processa modica caroli*	coastal epibenthic						8	25.00	0.04 ± 0.08	12.50	0.01 ± 0.01
Processa modica modica	coastal epibenthic	1	20.00	0.02 ± 0.05			1	12.50	0.01 ± 0.01		
Processa nouveli	coastal epibenthic	3			23.08	0.05 ± 0.10	27	87.50	0.12 ± 0.13	50.00	0.03 ± 0.03
Processa spp.	oceanic epibenthic	35	20.00	0.07 ± 0.16	61.54	0.50 ± 0.57	78	87.50	0.40 ± 0.53	87.50	0.11 ± 0.11
Processa? elegantula	coastal epibenthic	3			15.38	0.06 ± 0.16	7	37.50	0.04 ± 0.07		
**Stenopus spinosus*	cosmopolite epibenthic						4	37.50	0.02 ± 0.02		
HERMIT CRABS (Paguridae and Diogenidae)											
Anapagurus spp.	cosmopolite epibenthic	25	20.00	0.01 ± 0.03	38.46	0.42 ± 0.71	20	50.00	0.02 ± 0.02	50.00	0.10 ± 0.12
**Calcinus tubularis*	intertidal epibenthic						144	87.50	0.44 ± 0.89	12.50	0.01 ± 0.02
**Clibanarius erythropus*	intertidal epibenthic						2	12.50	0.01 ± 0.02		
**Dardanus arrosor*	coastal epibenthic						7	37.50	0.02 ± 0.03	12.50	0.01 ± 0.02
**Diogenes pugilator*	intertidal epibenthic						6	37.50	0.03 ± 0.05		
**Nematopagurus longicornis*	oceanic epibenthic						8	12.50	0.01 ± 0.02	37.50	0.05 ± 0.07
**Pagurus cuanensis*	coastal epibenthic						1	12.50	0.01 ± 0.02		
Pagurus spp.	cosmopolite epibenthic	16	20.00	0.04 ± 0.08	53.85	0.24 ± 0.27	11	50.00	0.03 ± 0.04	25.00	0.01 ± 0.02
GHOST SHRIMPS (Axiidea and Gebiidea)											
**Callianassa subterranea*	endobenthic						1	12.50	0.01 ± 0.01		
Callianassidae n.id.	endobenthic	1			7.69	0.01 ± 0.03	6	50.00	0.04 ± 0.05		
**Necallianassa truncata*	endobenthic						7			37.50	0.05 ± 0.08
**Upogebia deltaura*	endobenthic						2	12.50	0.01 ± 0.04		
**Upogebia pusilla*	endobenthic						1	12.50	0.00 ± 0.01		
**Upogebia spp.*	endobenthic						1	12.50	0.01 ± 0.01		

SLIPPER LOBSTER (Scyllaridae)																				
**Scyllarides latus*	coastal epibenthic										1	12.50	0.01	±	0.01					
**Scyllarus arctus*	coastal epibenthic										2	12.50	0.01	±	0.04					
**Scyllarus pygmaeus*	coastal epibenthic										1	12.50	0.01	±	0.01					
Scyllarus spp.	coastal epibenthic	1					7.69	0.01	±	0.05	8	12.50	0.02	±	0.06	37.50	0.02	±	0.04	
SQUAT LOBSTERS (Galatheidae, Porcellanidae and Polychelidae)																				
Galathea dispersa	coastal epibenthic	1					7.69	0.02	±	0.06	5					37.50	0.02	±	0.03	
Galathea FSL21	-	1					7.69	0.01	±	0.05	19	50.00	0.09	±	0.16	37.50	0.04	±	0.07	
Galathea intermedia	coastal epibenthic	9					46.15	0.13	±	0.19	2	25.00	0.01	±	0.03					
Galathea n.id.	coastal epibenthic	2						0.03	±	0.07	2	25.00	0.01	±	0.02					
Galathea S22	-	1	20.00	0.04	±	0.08					24	87.50	0.15	±	0.21					
Polychelidae n. id.	oceanic epibenthic	2					7.69	0.01	±	0.02	21	25.00	0.02	±	0.03	50.00	0.04	±	0.07	
CRABS (Brachyura)																				
**Acanthonyx lunulatus*	coastal epibenthic										5	12.50	0.02	±	0.04					
^Achaeus cranchii	coastal epibenthic	1					7.69	0.01	±	0.05										
**Atelecyclus rotundatus*	coastal epibenthic										4	25.00	0.01	±	0.02	12.50	0.01	±	0.02	
**Atelecyclus sp.*	coastal epibenthic										1					12.50	0.01	±	0.02	
Bathynectes spp.	coastal nektobenthic	6	20.00	0.04	±	0.08	30.77	0.08	±	0.15	1					12.50	0.01	±	0.02	
Brachyura n.id.	-	4	20.00	0.04	±	0.08	15.38	0.04	±	0.10	6	25.00	0.02	±	0.06	25.00	0.01	±	0.02	
**Calappa granulata*	oceanic epibenthic										41	62.50	0.13	±	0.20	25.00	0.01	±	0.02	
**Carcinus aestuarii*	intertidal epibenthic										1					12.50	0.01	±	0.02	
**Corystes cassivelaunus*	coastal epibenthic										1	12.50	0.01	±	0.02					
**Distolambrus maltzami*	oceanic epibenthic										1	12.50	0.01	±	0.02					
**Dorhynchus thomsoni*	oceanic epibenthic										1	12.50	0.01	±	0.01					
Ebalia spp.	oceanic epibenthic	26	20.00	0.15	±	0.33	53.85	0.34	±	0.54	78	100.00	0.32	±	0.23	87.50	0.07	±	0.05	
**Ergasticus clouei*	oceanic epibenthic										5					25.00	0.03	±	0.06	
**Eriphia verrucosa*	intertidal epibenthic										1	12.50	0.01	±	0.01					
**Ethusa mascarone*	coastal epibenthic										4	25.00	0.02	±	0.04					
^Eurynome spp.	coastal epibenthic	3					23.08	0.05	±	0.09										
Goneplax rhomboides	coastal epibenthic	172					76.92	2.94	±	4.32	37	62.50	0.22	±	0.25	37.50	0.01	±	0.02	
*Heterotremata	-										1	12.50	0.01	±	0.01					
**Homola barbata*	cosmopolite epibenthic										4	25.00	0.01	±	0.01	25.00	0.01	±	0.03	
**Ilia nucleus*	coastal epibenthic										5					50.00	0.03	±	0.04	
^Liocarcinus depurator	intertidal epibenthic0	2					7.69	0.04	±	0.16										
Liocarcinus spp.	intertidal epibenthic0	33					69.23	0.51	±	0.80	23	87.50	0.07	±	0.05	37.50	0.04	±	0.06	
**Macropodia sp.*	coastal epibenthic										1	12.50	0.01	±	0.02					
**Maja sp.*	coastal epibenthic										2	12.50	0.01	±	0.02					
**Maja squinado*	coastal epibenthic										1	12.50	0.01	±	0.01					
Majidae n.id.	coastal epibenthic	2	20.00	0.04	±	0.08	7.69	0.02	±	0.08	7	12.50	0.01	±	0.01	25.00	0.04	±	0.07	
**Monodaeus couchii*	oceanic epibenthic										50	87.50	0.27	±	0.33	12.50	0.01	±	0.02	
**Nepinnotheres pinnotheres*	coastal epibenthic										9	37.50	0.03	±	0.05					
**Pachygrapsus marmoratus*	intertidal epibenthic										2					25.00	0.01	±	0.02	
**Pachygrapsus spp.*	intertidal epibenthic										15	37.50	0.05	±	0.10	25.00	0.01	±	0.02	
Parthenope spp.	cosmopolite epibenthic	11					38.46	0.13	±	0.22	81	100.00	0.33	±	0.20	62.50	0.06	±	0.09	
Pilumnus spp.	coastal epibenthic	2					7.69	0.04	±	0.16	12	50.00	0.04	±	0.05					
**Pirimela denticulata*	coastal epibenthic										1	12.50	0.01	±	0.02					
*Plagusiidae n.id.	coastal epibenthic										8	12.50	0.03	±	0.07					
Polybiidae n.id.	coastal nektobenthic	19	20.00	0.04	±	0.08	30.77	0.35	±	1.08	2	25.00	0.01	±	0.02					
*Porcellanidae n.id.	coastal epibenthic										1	12.50	0.01	±	0.01					
*Portunidae n.id.	-										23	12.50	0.01	±	0.02	50.00	0.15	±	0.19	
**Thia scutellata*	coastal epibenthic										3	25.00	0.02	±	0.04					
Xantho spp.	coastal epibenthic	1					7.69	0.01	±	0.05	102	100.00	0.33	±	0.64	25.00	0.01	±	0.02	
*Xanthoidea n. id.	-										1	12.50	0.01	±	0.01					
Total		2679		24.60	±	14.17		17.25	±	12.08	4769		14.45	±	6.85		8.53	±	7.43	

14 Table 2. The seasonal number of decapods larvae (N), their seasonal and area (northern
15 and southern stations) frequency of occurrence (F) and the average density (ρ) over the
16 water column (number of larvae/100 m^3 ± SD) of the different taxa identified, during
17 late autumn (2009) and summer (2010). A classification of the different taxa according
18 to their adult habitats is provided.
19 *(^)Exclusively autumn appearance and (*) exclusively summer appearance*
20

Adult habitat	Cluster A	Cluster ASshelf	Cluster S	Cluster SSslope
Mesopelagic	74.78%	22.55%	18.83%	48.78%
Epipelagic			16.10%	16.62%
Coastal necktobenthic		17.73%	16.46%	
Coastal epibenthic		18.86%		

Table 3. Similarities among cluster assemblages regarding taxa composition grouped by their adult habitat. Only the groups that represent more than 50% of the cumulative contribution to explain the variability of each seasonal Cluster group (SIMPER) are included.

(A:late Autumn; ASshelf:late Autumn Souternh shelf break; S: Summer; SSslope: Summer Southern mid slope)

		Factor		Variables		
Season	**Adult habitat**	**area**	**station**	**fluo**	**temp**	**sal**
Late autumn	Mesopelagic & epipelagic	***	ns	***	***	ns
	Coastal epibenthic & nektobenthic	***	***	***	ns	ns
Summer	Mesopelagic & epipelagic	ns	ns	***	ns	***
	Coastal epibenthic & nektobenthic	***	***	***	***	***

Table 4. Effect of fluorescence (fluo), temperature (temp) and salinity (sal) on the density of late zoeas/protozoeas (stage 2) over the water column as estimated from a generalized linear model. Area and station (shelf break or mid slope) are included in the model as factors. Results are shown for late autumn and summer for the larvae classified by their adult habitat. The asteriscus *** indicate significant effects ($p<0.001$)

No significance "ns"= p>0.001

		Factor		Variables		
Season	**Functional group**	**area**	**station**	**fluo**	**temp**	**sal**
Autumn	Mesopelagic & epipelagic	***	***	ns	***	***
	Coastal epibenthic & nektobenthic	***	ns	***	ns	ns
Summer	Mesopelagic & epipelagic	***	***	***	***	ns
	Coastal epibenthic & nektobenthic	***	***	***	ns	***

Table 5: Effect of fluorescence (fluo), temperature (temp) and salinity (sal) on the density of early zoeas/protozoeas (stage 1) estimated from a generalized linear model. Area and station (shelf break or mid slope) are included in the model as factors. Results are shown for late autumn and summer for the larvae classified by their adult habitat. The asteriscus *** indicate significant effects ($p<0.001$)

No significance "ns"= p>0.001

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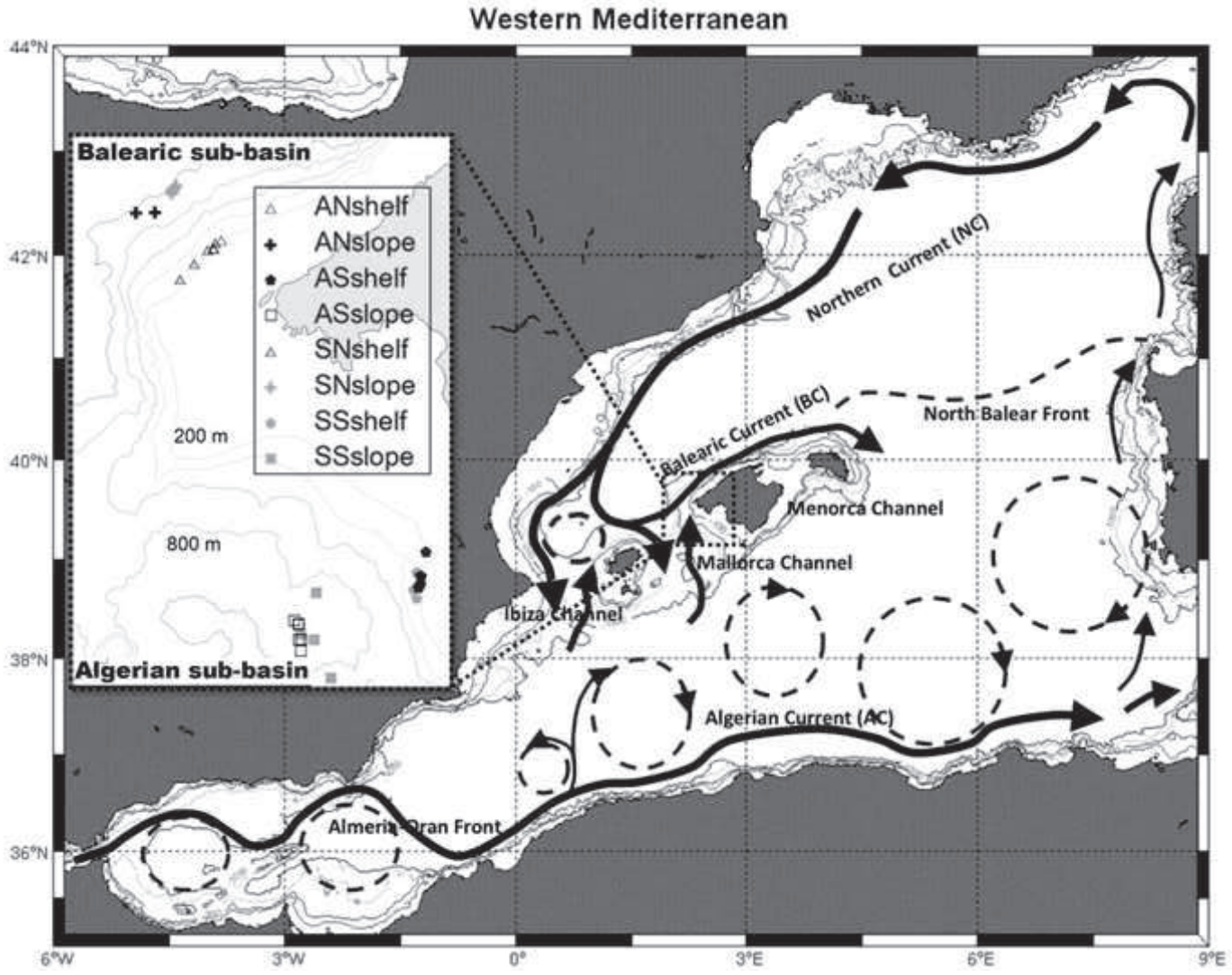

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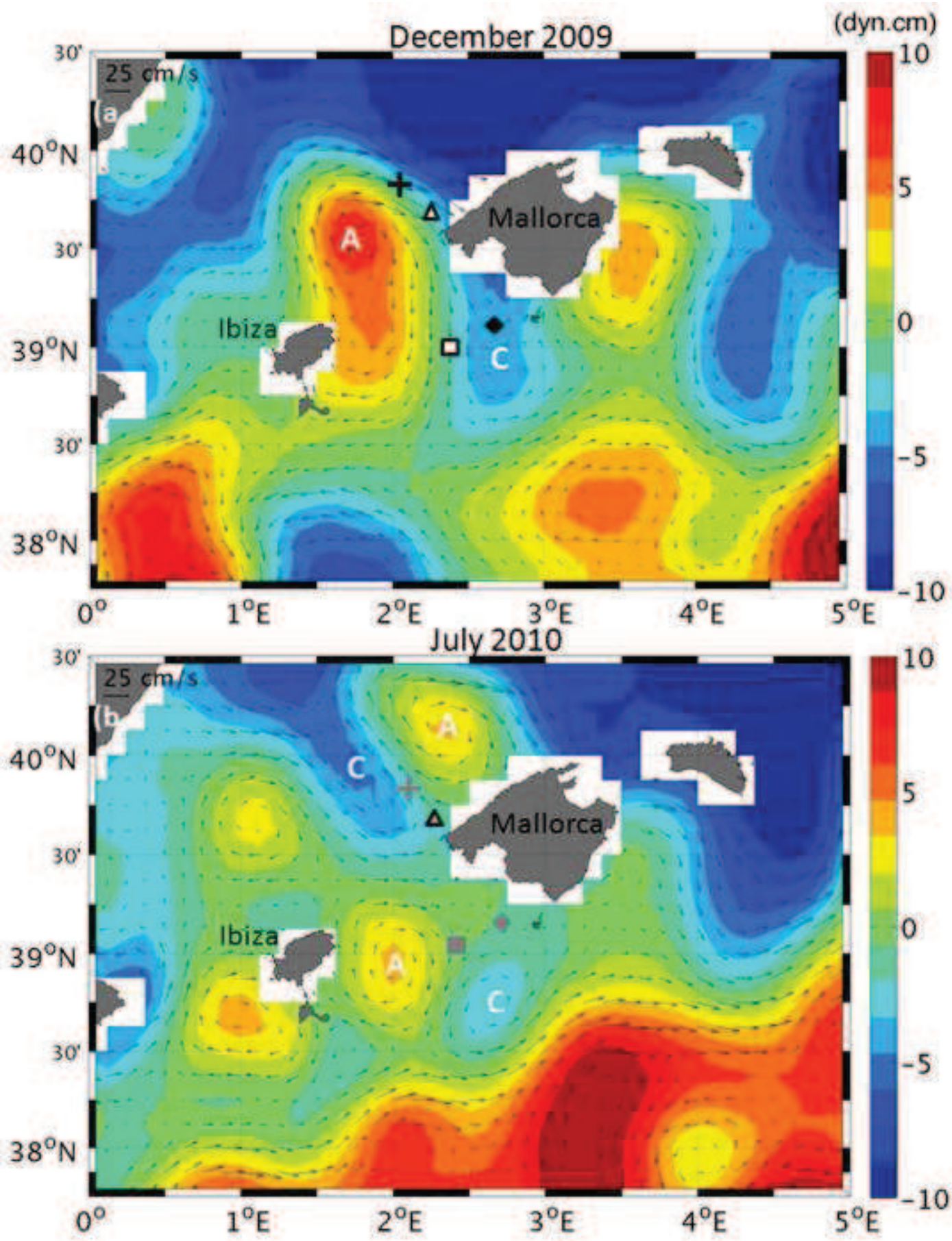

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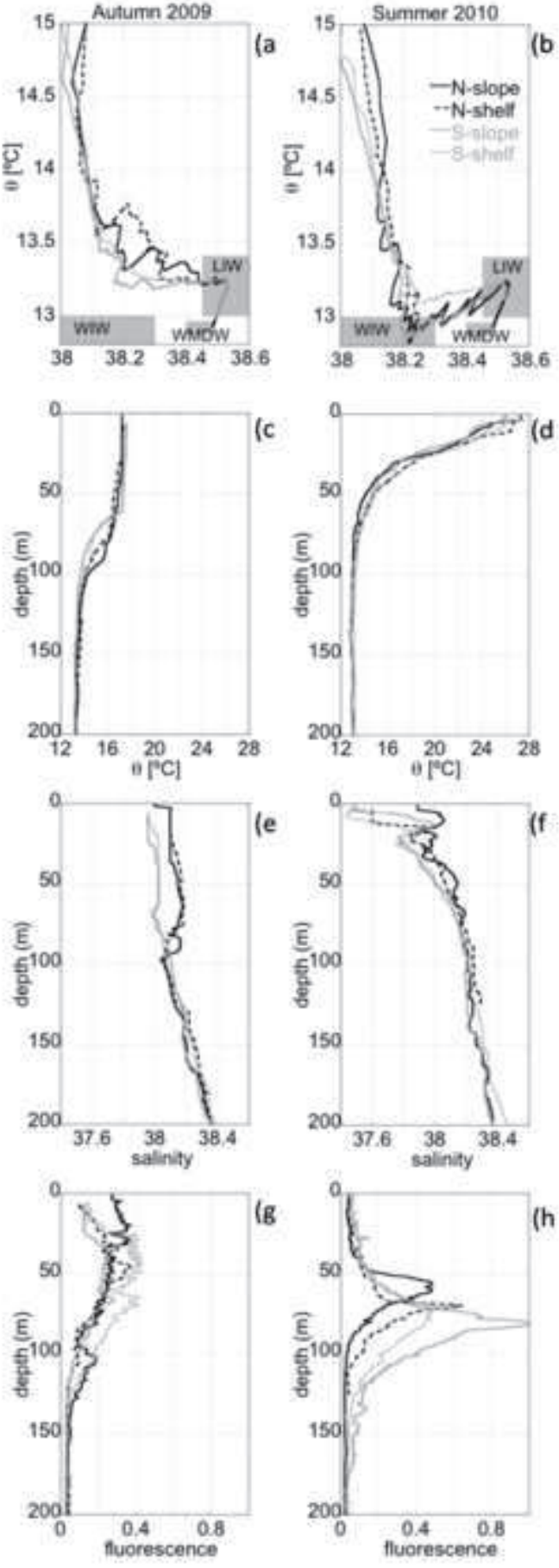

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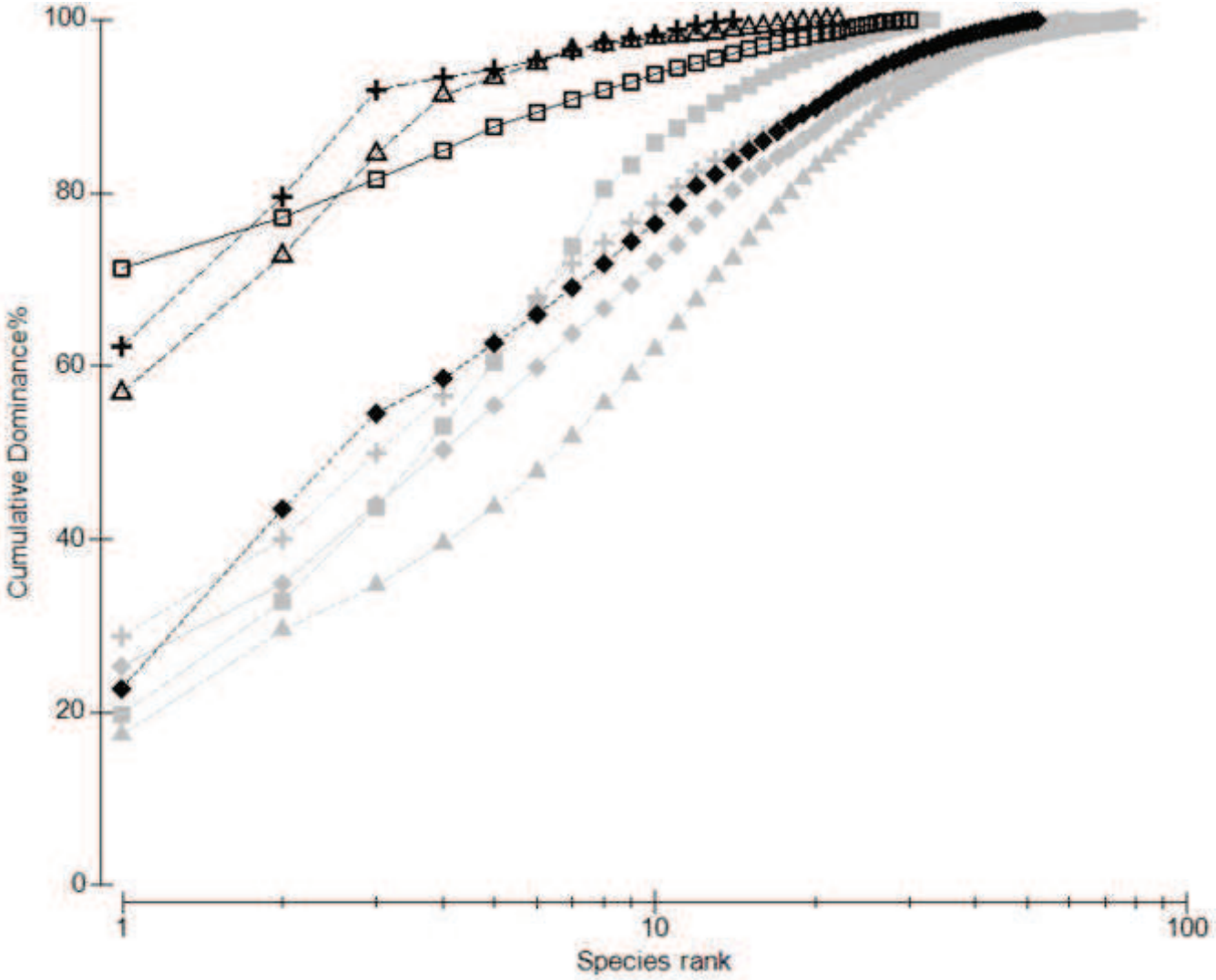

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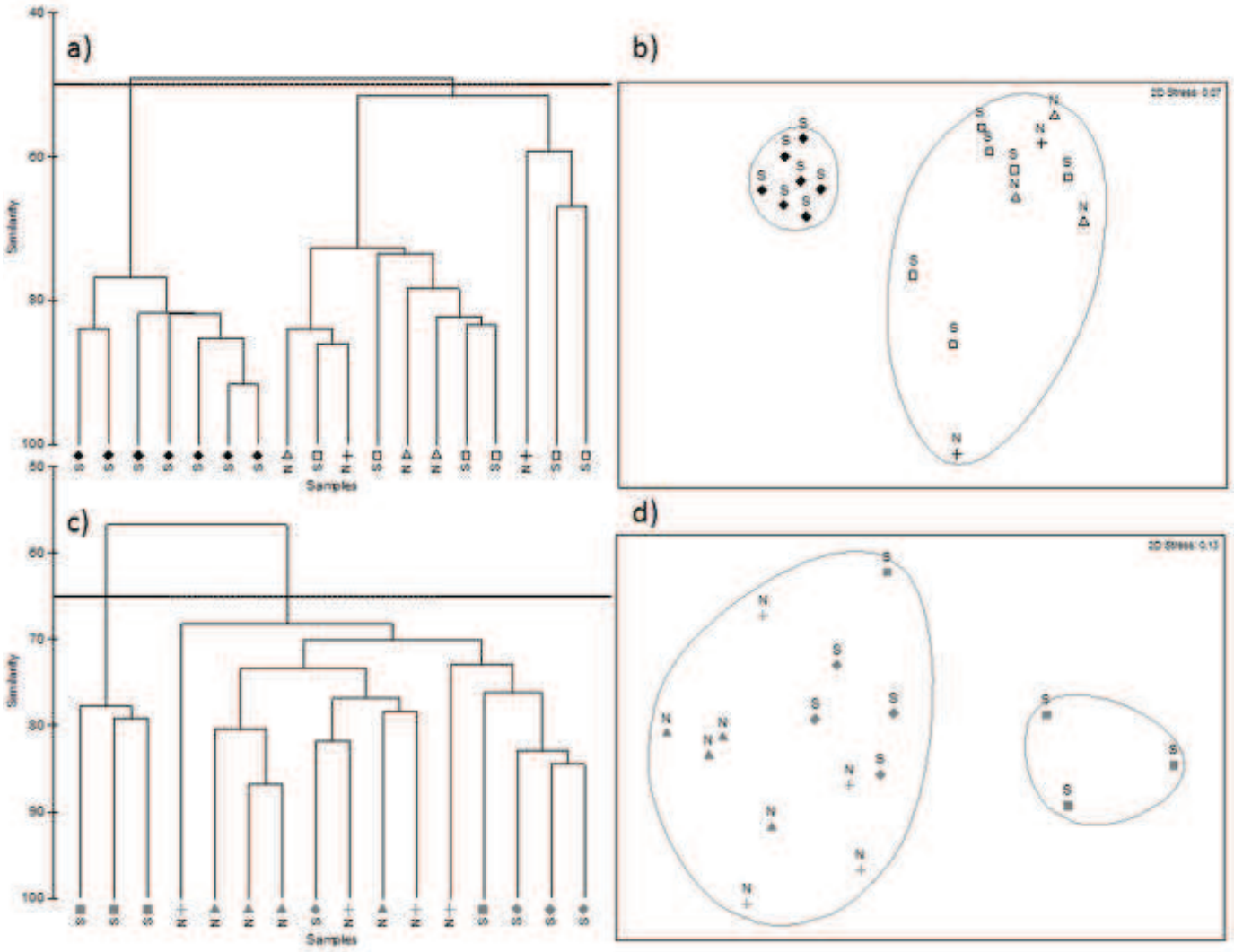

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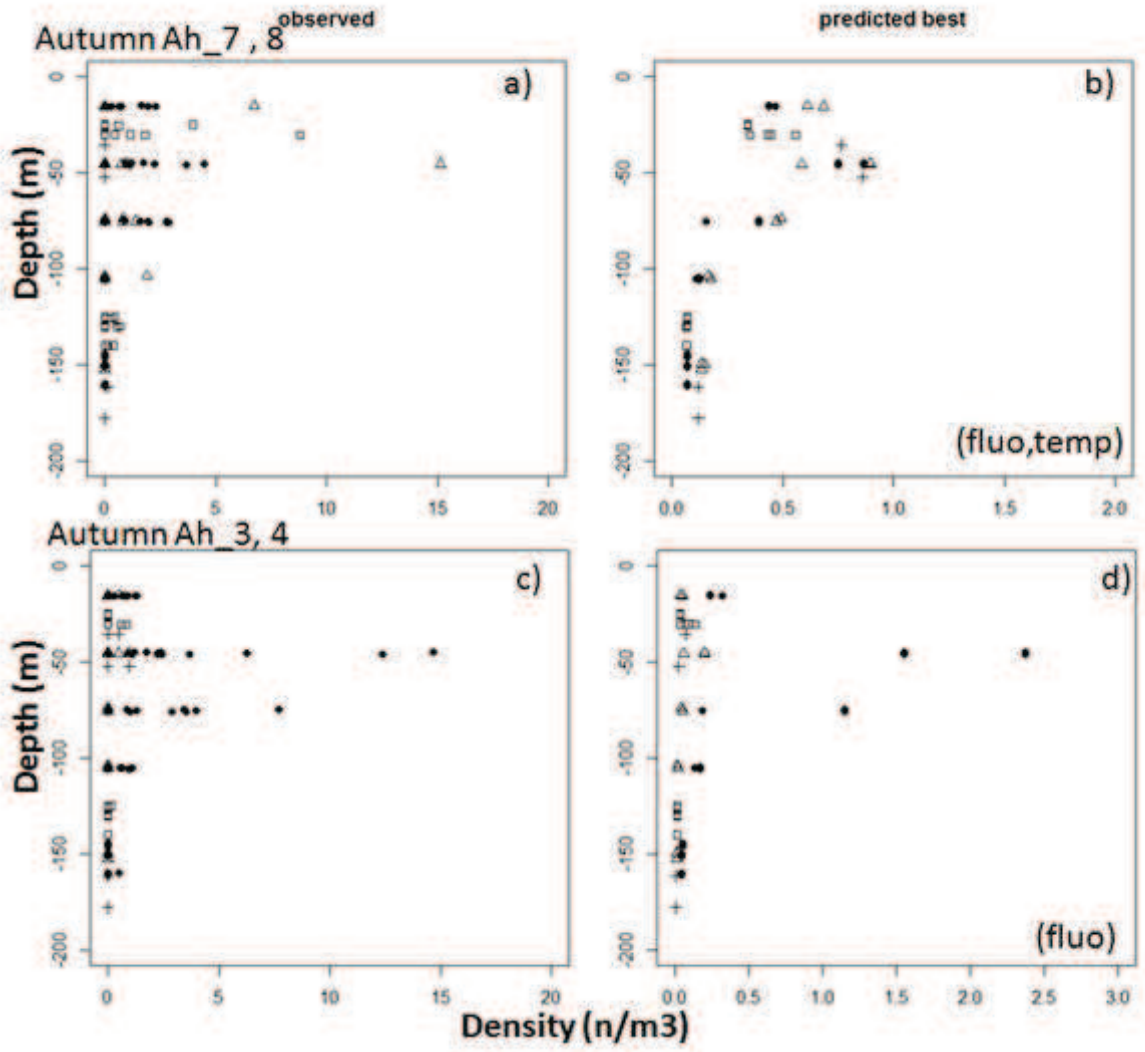

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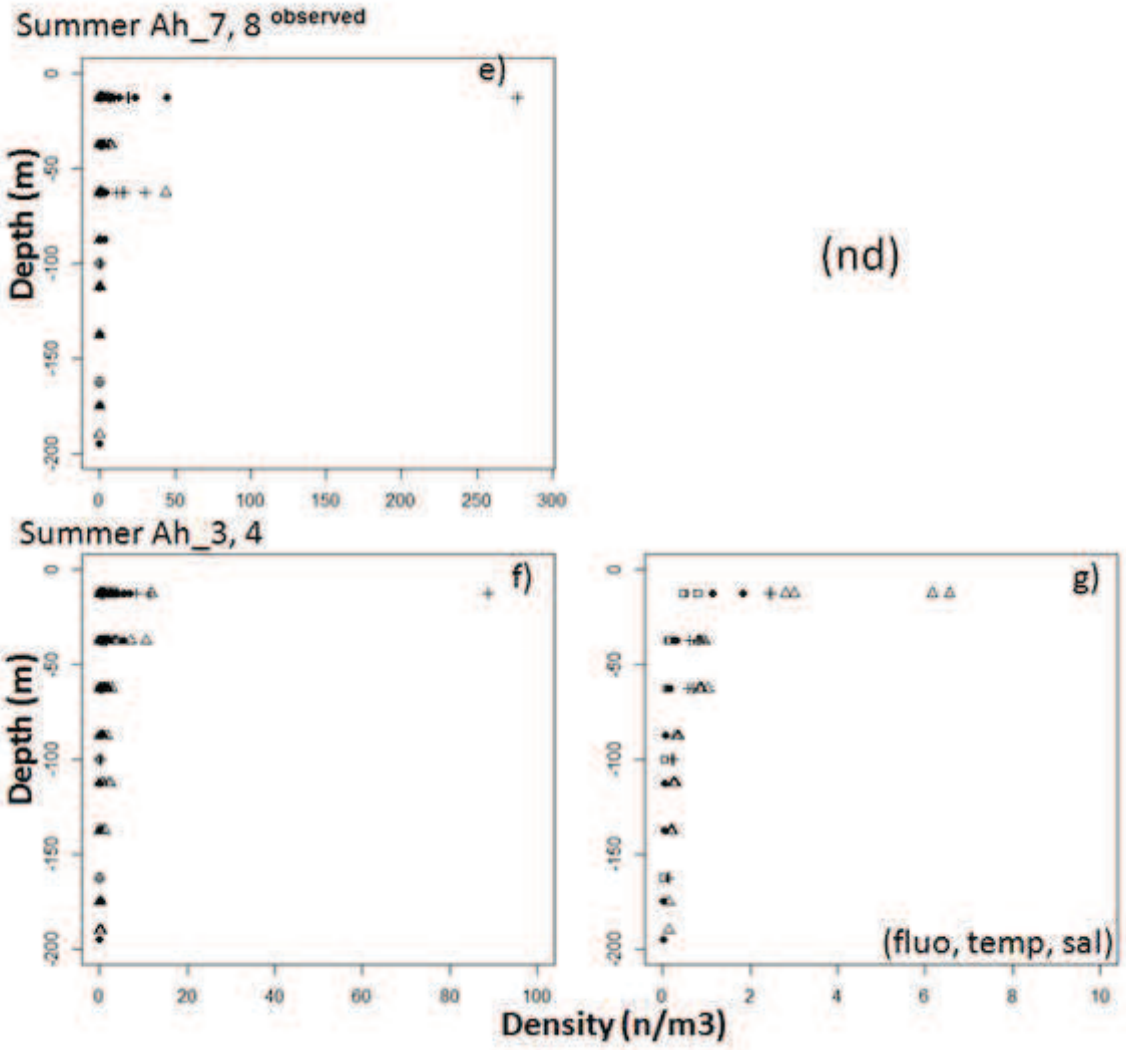

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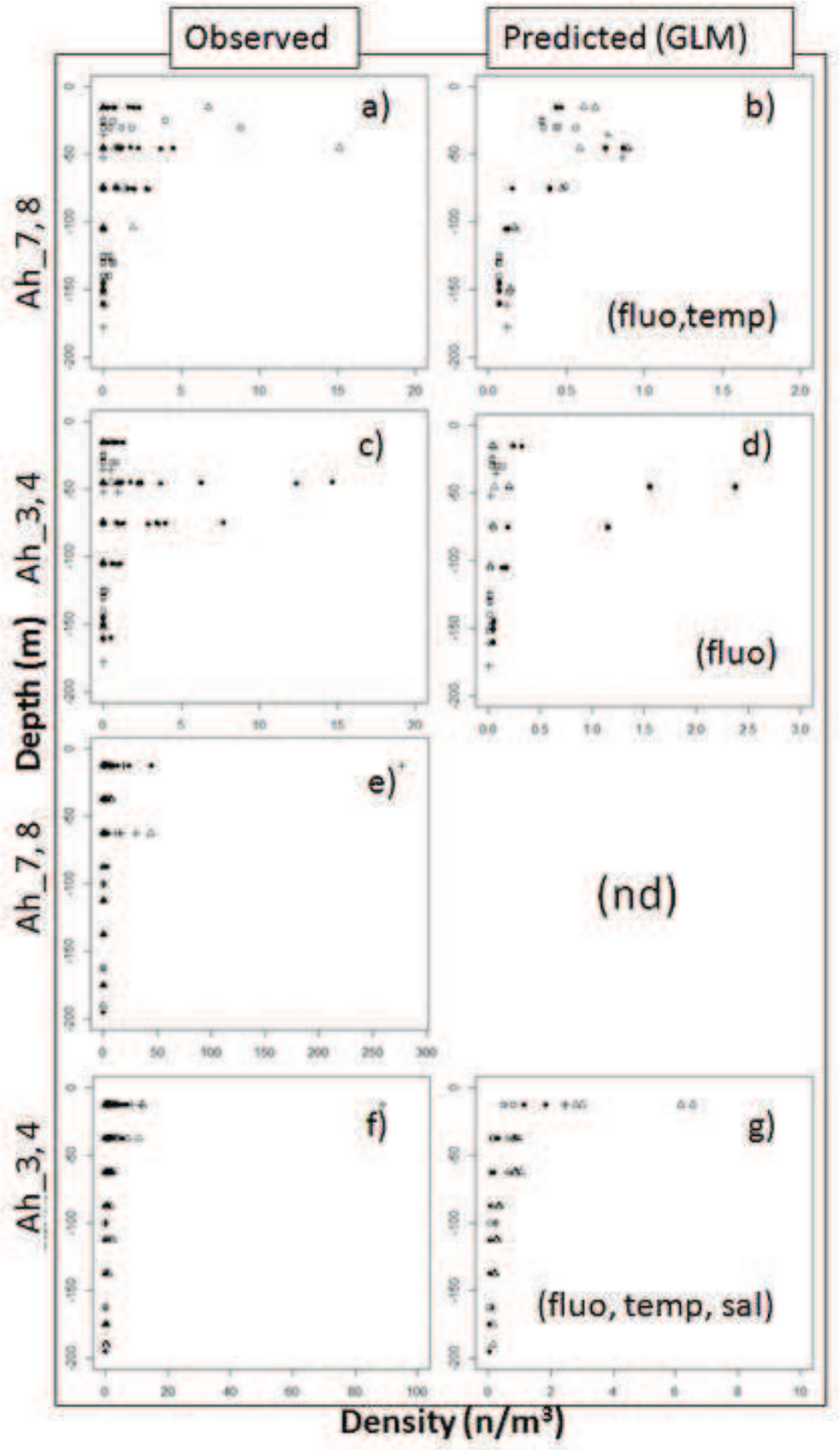

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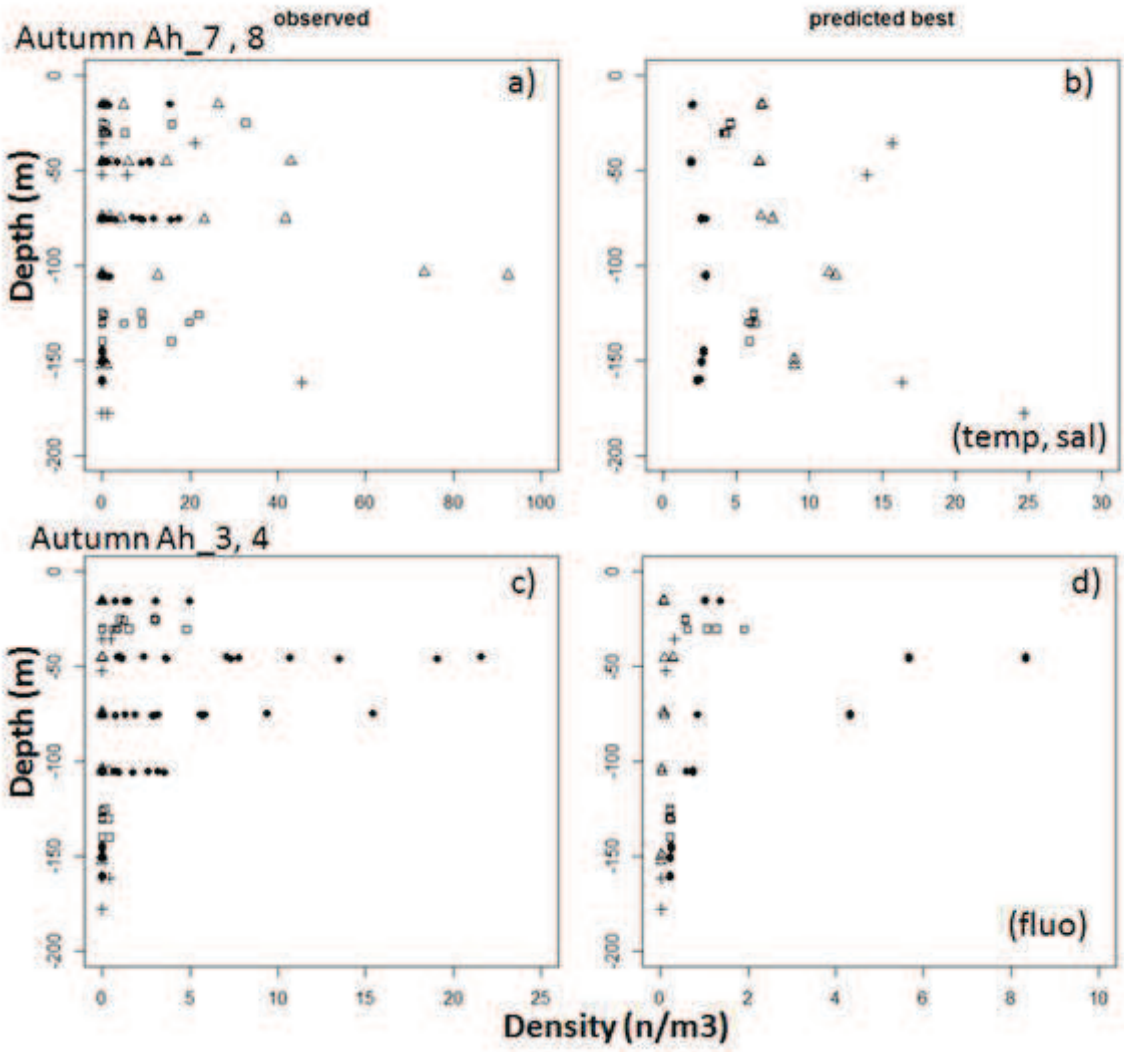

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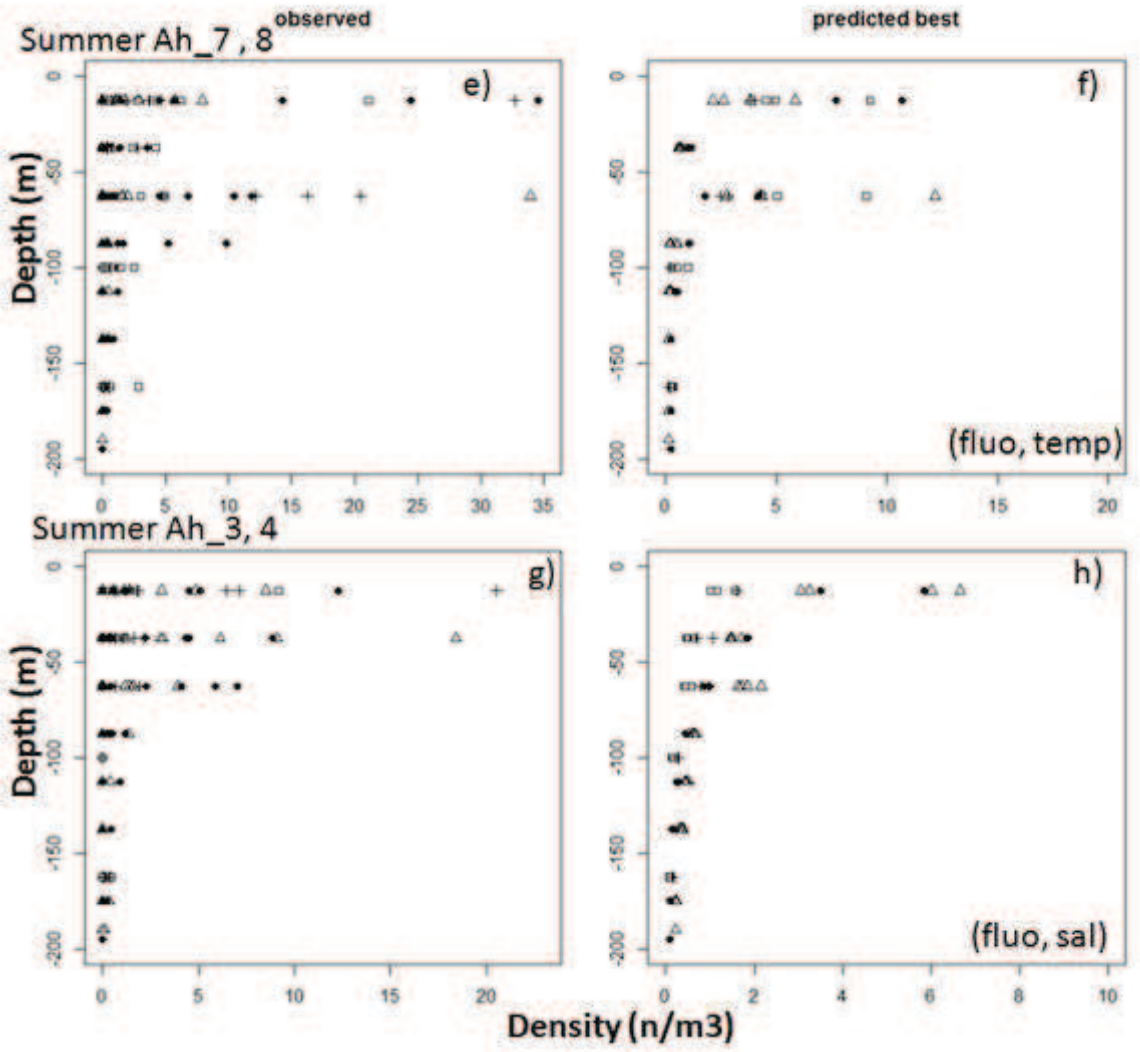

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